

BIOGEOGRAPHY OF THE OPISTHOBRANCH GASTROPOD FAUNA OF SOUTHERN AFRICA

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ABSTRACT

In temperate Atlantic and Indian Ocean waters of southern Africa, endemic and Atlantic opisthobranch mollusks are predominant, while in tropical waters of the region these are replaced by Indo-Pacific and circumtropical species. Well-defined boundaries, previously described for southern African biogeographical provinces, are blurred when opisthobranchs are considered. However, distinct temperate and tropical faunas are present. Most of the Indo-Pacific species present in southern Africa extend well across the Indian Ocean, and a majority of species are also found on the non-marginal portions of the Pacific Plate.

Sister group relationships suggest that the southern African opisthobranch fauna is phylogenetically and biogeographically linked to three primary regions: sub-Antarctic, North Atlantic and Indo-Pacific. Links with sub-Antarctic species appear to be the oldest and may be related to cold water present during the Pliocene. Relationships with North Atlantic species are more recent (Pleistocene) and also appear to be related to major oceanographic and climatic changes.

Levels of endemism between opisthobranch and prosobranch gastropods differ and appear to be related to differing life history strategies. Contrary to the view of some authors, that large discrepancies in levels of endemism in different taxa are simply systematic artifacts, these discrepancies could actually represent challenges to simplistic vicariant hypotheses. The notion that sister species relationships of endemic species provide the only meaningful biogeographical data is discussed and challenged.

Southern Africa represents a region that is crucial to the understanding of marine biogeography. The convergence of the Atlantic and Indian Oceans, characterized by water masses of divergent physical oceanographic characteristics, accentuates the geographical importance of this region. This variation of temperature regimes and oceanic currents supports a rich marine biota with phylogenetic and biogeographical links to species in other southern oceans, the northern Atlantic and the Indo-Pacific tropics.

Previous studies on the distribution of the marine biota of southern Africa have been largely descriptive and have attempted to characterize the species composition of the region and to delimit biogeographical provinces (Ekman, 1953; Macnae and Kalk, 1958; Day, 1967; Briggs, 1974; Griffiths, 1974; Brown and Jarman, 1978; Millard, 1978; Kensley, 1981, 1983; Kilburn and Rippey, 1982). An excellent description of the biological and physical oceanographic characteristics of the region was provided by Brown and Jarman (1978) and will not be repeated here.

Vicariance biogeographical theory (Croizat, 1958; Croizat *et al.*, 1974; Nelson, 1978; Nelson and Platnick, 1981; Springer, 1982) provides additional historical perspectives and suggests causes of geographical isolation that must also be taken into consideration.

Most opisthobranch gastropods have planktonic veliger larvae, which are induced to metamorphose from a pelagic to a benthic existence by the presence of an environmental cue, generally a specific biochemical product produced by the adult food source (Hadfield and Karlson, 1969; Harris, 1975; Switzer-Dunlap and Hadfield, 1977; Bonar, 1978). In the absence of this cue, larvae of many species can delay metamorphosis for variable periods and continue to filter-feed in the plankton until the cue is present, or until they lose their viability and die. This plasticity provides a potential for gastropod larvae to be transported long distances by oceanic currents and, in some cases, to cross entire ocean basins (Scheltema, 1971a, b, 1972; Kempf, 1981). Direct development, in which the larva undergoes its entire

embryonic and larval development within a benthic egg capsule and is never planktonic, is rare in opisthobranch gastropods and has been reported in about a dozen species (Hadfield, 1963; Bridges, 1975; Bonar, 1978; Gosliner and Griffiths, 1981; Rose, 1985). Prosobranch gastropods exhibit the same range of developmental modes that opisthobranchs do, but direct development and short-term planktonic development are the dominant patterns in many taxa (Fretter and Graham, 1962; Morton, 1968; Webber, 1977). Scheltema and Williams (1983) have suggested that closely related marine organisms with differing life-history modes can have different distributional patterns that are directly related to their relative dispersal capabilities. One might expect that opisthobranchs, with few species having direct or short-term development, would exhibit less endemism and more widespread distributions than do prosobranch gastropods.

This paper examines the distribution patterns exhibited by opisthobranch gastropods in southern Africa and compares them with those described previously for other marine taxa. The universality of biogeographical boundaries within the region is discussed. The relative importance of possible vicariant events and subsequent dispersal in the evolution of the opisthobranch fauna of southern Africa is considered. The relevance of differences in levels of endemism as an indicator of the validity and applicability of vicariant hypotheses is discussed.

METHODS

SOURCES OF DATA

The Opisthobranchia studied here include representatives of all the major benthic orders of the subclass. Members of the Pyramidellidae have been recently excluded from the Opisthobranchia (Gosliner, 1981a), and are excluded from this study. The holoplanktonic Thecosomata and Gymnosomata are poorly documented from southern African waters and are not included in the present examination. No members of the Acochlididae have been recorded from southern Africa.

At first appearance, the opisthobranch fauna of southern Africa appears to be well studied (Linnaeus, 1767; Quoy and Gaimard, 1823; Rang, 1828; Krauss, 1848; Stimpson, 1854; Gould, 1859; Sowerby, 1873, 1892, 1894, 1897; Martens, 1879; Watson, 1886; Pelseneer, 1888; Gilchrist, 1900; Vayssière, 1900; Smith, 1902, 1903, 1910; Eliot, 1905, 1910; Meisenheimer, 1905; Bergh, 1907; Thiele, 1912, 1925; Bartsch, 1915; Tomlin, 1920; Barnard, 1927, 1932, 1933, 1934, 1963a, b; O'Donoghue, 1929; Turton, 1932; Macnae, 1954a, b, 1955, 1957, 1958, 1962a, b; Macnae and Kalk, 1958; Thompson, 1979; Thompson and Brown, 1981; Gosliner, 1981b, 1982, 1985; Gosliner and Griffiths, 1981; Ev. Marcus and Gosliner, 1985; Millen and Gosliner, 1984; Gosliner, 1985; Griffiths, 1985). Approximately 209 species of opisthobranchs from South Africa and Mozambique have been recorded. I conducted field observations spanning a three year period from November 1979 to November 1982, and in May 1984 along much of the southern African coast from Lamberts Bay on the Atlantic coast to Kosi Bay on the

South African-Mozambique border. Material was collected from the intertidal zone and the subtidal zone. Subtidal collections were made by means of scuba diving to a depth of 40 m and by trawling and dredging to a depth of 90 m. These investigations yielded specimens of 190 species of opisthobranchs not previously recorded from southern Africa, including 120 undescribed species. Although a large percentage of species within southern Africa is undescribed, reliable distributional data from a wide geographical area are available for many of them. Previously unpublished distributional data for these species are included in the analysis presented here.

Other unpublished records of opisthobranch mollusks have also been incorporated in this study. These include collections from Madagascar, Reunion Island and Tanzania by Michael Gosliner and Gary Williams, my own data collected from the Seychelles and Hawaiian Islands and material from the collections of the Division of Mollusks, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

DEFINITIONS

Southern Africa, for the purposes of this study, includes the region south of 15° S latitude, from Mocamedes, Angola, on the Atlantic coast, to Mozambique Island in the Indian Ocean. Employing these limits is expedient for two reasons: most other studies of the faunas of southern Africa are restricted to these geographical limits (Barnard, 1950; Kensley, 1981), and few data are available for the areas immediately to the north of these limits.

Many terms used in biogeographical studies have ambiguous meanings and have been the cause of misinterpretation. For this reason, their specific applicability to the scope of this paper is explained. The term endemic, in the present context, applies to species that are believed to be restricted to southern Africa. Circumtropical species are here defined as those recorded from at least some portion of each of the tropical Atlantic, Indian and Pacific Oceans. Indo-Pacific species are those recorded from at least some portion of the tropical Indian and Pacific Oceans, but not from the Atlantic Ocean. Indo-West Pacific species, following Springer (1982), are differentiated from Indo-Pacific species by being present throughout the Indian Ocean, but only in the western margin of the Pacific Plate. Cosmopolitan species are regarded as being widespread, not limited to tropical or temperate regions. Atlantic species are those found in some portion of the Atlantic Ocean aside from the coast of southern Africa.

For the purposes of this study, species are placed in the broadest applicable geographic classification. For example, a species found in South Africa, East Africa, the Hawaiian Islands and Brazil would be considered to have a circumtropical distribution.

SELECTION OF GEOGRAPHICAL SITES

Virtually all previous workers who have studied the marine biota of southern Africa have concluded that there are several distinct biogeographical provinces within the region (see Brown and Jarman, 1978; Kensley, 1981; Kilburn and Rippey, 1982), with varying degrees of overlap between them. It is, therefore, less informative to present distributional

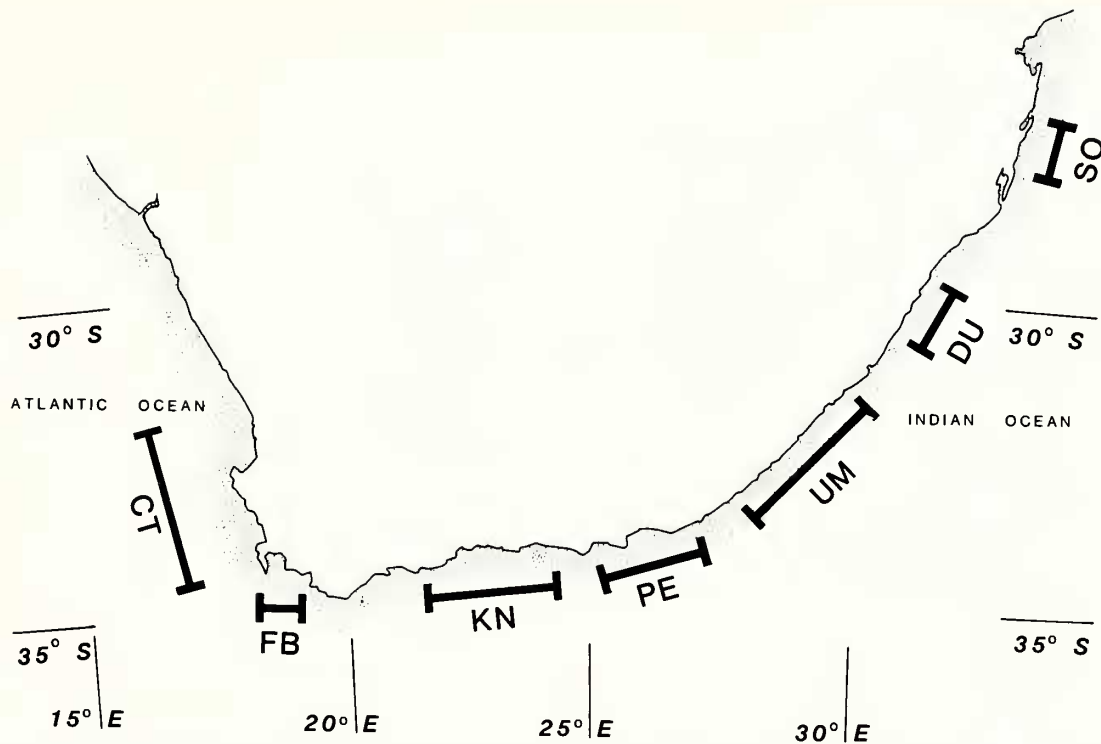


Fig. 1. Geographical regions examined in this study (CT - Cape Town, FB - False Bay, KN - Knysna, PE - Port Elizabeth, UM - Umgazana, DU - Durban, SO - Sodwana Bay).

data for the entire region as a single fauna. Rather, it is appropriate to define different geographical areas in order that their biogeographical affinities may be contrasted. Seven areas (Fig. 1) were selected in order that comparisons can be made. They represent most of the previously described variation in oceanographic conditions and include the geographic extent of the region. In addition, these areas were selected because they have been reasonably well studied and are likely to reflect an accurate sample of the total opisthobranch fauna of the region. The areas chosen are centered at Cape Town (Lamberts Bay to Cape Point), False Bay (Buffle's Bay to Rooi Els), Knysna (Still Bay to Storm's River Mouth), Port Elizabeth (Jeffreys Bay to Port Alfred), Umgazana (Gonubie to Port St. Johns), Durban (Park Rynie to Salt Rock) and Sodwana Bay (Adlam's Reef to Kosi Bay). The localities in parentheses represent the geographical limits of each area considered. Not all areas are of equal size nor have they been sampled with equal intensity. For example, virtually no sublittoral samples have been collected from Umgazana. Despite these potential biases, several distinct patterns emerge.

RESULTS

Distributional data within southern Africa and outside the region are presented for 237 species of opisthobranchs (Appendix 1). The percentages of endemic, circumtropical, Indo-Pacific, Atlantic and cosmopolitan species present in each of the seven regions are compared (Fig. 2). Several ob-

vious trends emerge when these data are compared. There is a high incidence of endemism in the southwestern portion of southern Africa, which abruptly diminishes in the localities to the east of Port Elizabeth. There is also a small percentage of Indo-Pacific and circumtropical species present in the southwestern portion of southern Africa, which increases markedly in an eastward direction. A significant number of Atlantic species is found in the southwestern and south-eastern portions of the Cape Province but these are notably absent from Transkei and Natal localities.

Even more significant is the abrupt faunal shift in the geographical affinities between Port Elizabeth and Umgazana. In Cape Town, False Bay, Knysna and Port Elizabeth the majority of species are endemic or Atlantic. In Umgazana, Durban and Sodwana Bay most species are circumtropical or Indo-Pacific.

DISCUSSION

FACTORS THAT AFFECT BIOGEOGRAPHICAL CONCLUSIONS

Biogeographical studies are limited by the level of knowledge of the geographical area of immediate concern, and by the available data from adjacent or associated regions. This is certainly true of the opisthobranch fauna of southern Africa.

Relatively few studies have been conducted on the opisthobranch faunas of the west coast of Africa. Ev. Marcus and Er. Marcus (1966, 1968) recorded 19 species of

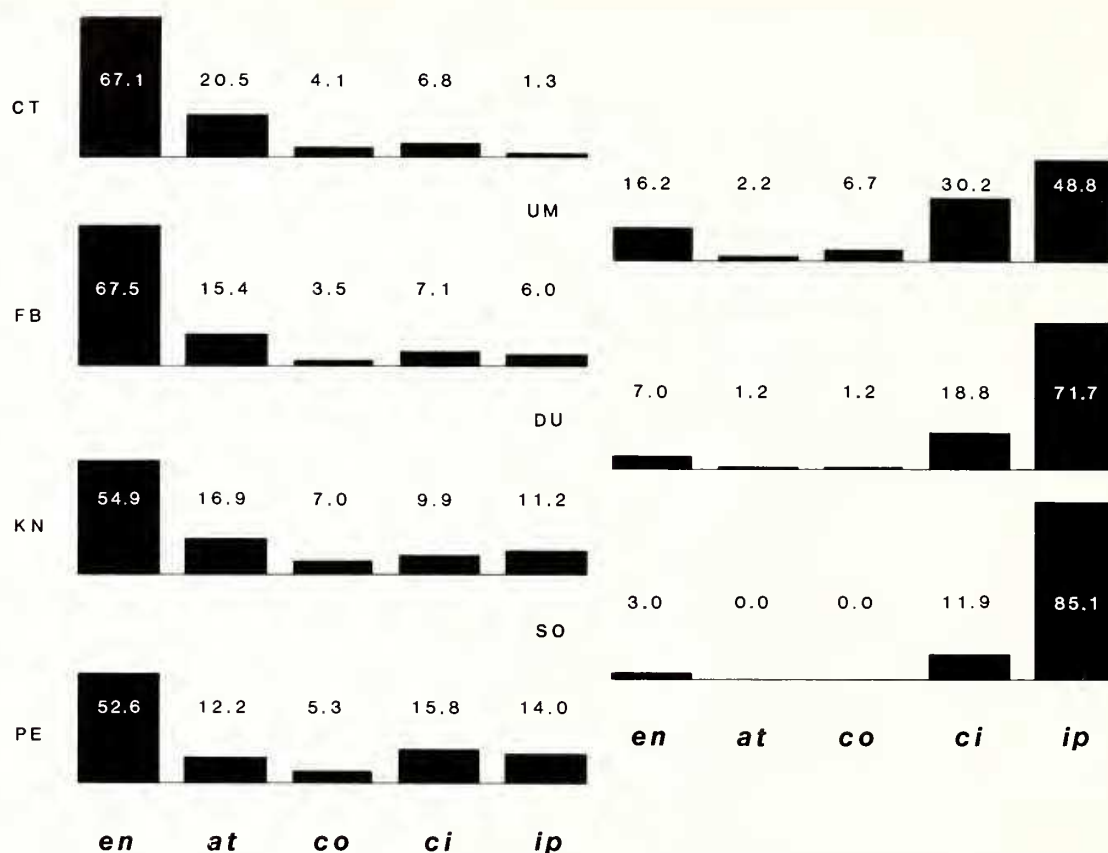


Fig. 2. Biogeographical affinities of southern African opisthobranchs within the seven regions studied (CT - Cape Town, FB - False Bay, KN - Knysna, PE - Port Elizabeth, UM - Umgazana, DU - Durban, SO - Sodwana Bay, en - endemic, at - Atlantic, co - cosmopolitan, ci - circum-tropical, ip - Indo-Pacific).

opisthobranchs from the Gulf of Guinea and six species from the Ivory Coast. Edmunds (1977, 1981) conducted the most comprehensive studies of West African opisthobranchs and recorded 46 species from Ghana. The only other locality that has been studied is Senegal, from which Pruvot-Fol (1953) recorded 11 species and Bouchet (1971) listed an additional three species.

Most of the coast of East Africa and the islands of Madagascar and Reunion have been poorly studied. Twenty-six species of opisthobranchs have been reported from Madagascar (Ev. Marcus and Er. Marcus, 1970), fourteen species from the Seychelles (Edmunds, 1972) and 35 species from Mauritius (Bergh, 1888, 1889). The portion of East Africa that has been most thoroughly investigated is the coast of Tanzania, including Zanzibar (Eliot, 1902, 1903a, b, 1904a, b, c; Edmunds, 1969, 1970, 1971; Edmunds and Thompson, 1972; Rudman, 1973a, b, 1977, 1978, 1979, 1980, 1981a, b, 1982a, b, 1984). Although about 200 species have been recorded in the literature, many more species occur there (Rudman, pers. comm.).

Lack of distributional information from areas surrounding a particular region, can lead to incorrect biogeographical conclusions, particularly in the case of erroneous assumptions of endemism.

Changes in the systematics of taxa can also alter

biogeographical conclusions. For example, *Aeolidiella saldanhensis* Barnard and *A. multicolor* Macnae were thought to represent distinct endemic species in southern Africa. Recent taxonomic revisions (Gosliner and Griffiths, 1981) demonstrated that both species are junior synonyms of a widespread, circumtropical species.

Another factor which should be considered in any biogeographical study is the potential alteration of natural distributional patterns by human intervention. The prey of opisthobranch gastropods are frequently colonial organisms such as hydroids, bryozoans and sponges, which are known to foul ships' hulls. Nudibranchs, often with their food and egg masses, can be transported long distances in this manner. These introduced species have limited ranges where they become established, and are generally restricted to harbors. There is no evidence that over time, they expand their ranges appreciably.

There appears to be at least one example of the introduction of an opisthobranch species into South African waters by this means. The natural range of *Catrina columbiana* (O'Donoghue) is from the Pacific coast of North America to Japan (Baba and Hamatani, 1963). In South Africa it has been found only in Cape Town Harbor and its presence there is probably a result of international shipping (Gosliner and Griffiths, 1981).

In another instance, *Thecacera pennigera* (Montagu) is known from England, Brazil, Ghana, Japan, Australia, New Zealand and South Africa. Willan (1976) suggested that the species owes much of its distribution to transport by shipping. However, *T. pennigera* is commonly found along the coast of southern Africa from Cape Town to Umgazana. While it is found in harbors, several localities are over 250 km from the nearest harbor. Though it is possible that this species could have been distributed more widely in southern Africa following its introduction, this scenario seems unlikely. Most species that are known to be introduced retain a restricted range for extensive periods of time. Willan and Coleman (1984) have similarly suggested that *Polycera hedgpethi* Er. Marcus, which is known from central California and Mexico, Australia, New Zealand and South Africa, has been introduced into Australia by shipping. The single locality where this species has been found in South Africa is the Keurbooms River Estuary, which is a shallow inlet devoid of major shipping. *P. hedgpethi* has not been found in any large harbor in southern Africa, despite concerted collecting efforts. In the cases of *T. pennigera* and *P. hedgpethi*, it therefore does not seem reasonable to ascribe their presence in southern African waters solely to human introduction.

DIVISION OF BIOGEOGRAPHICAL PROVINCES

Most studies of the biogeography of southern Africa have focused upon the subdivision of the coastline into biogeographical provinces (Stephenson, 1948; Day, 1967; Briggs, 1974; Griffiths, 1974; Brown and Jarman, 1978; Kensley, 1981). Kensley (1983) noted that these divisions are the subject of much controversy. Most of the above authors have considered the same five provincial areas: West African, cold Atlantic temperate, warm Indian temperate, subtropical east coast and tropical east coast. These areas overlap to varying degrees. Briggs (1974) distinguished two warm temperate provinces in southern Africa, bordered by tropical regions to the north.

While there are insufficient data to say much about the West African-Cold Temperate provincial boundary for opisthobranchs, data for other areas within the region suggest a great deal about provincial boundaries. Brown and Jarman (1978), noting that the Cape Peninsula separates the Atlantic Ocean from False Bay, emphasized that the temperature difference between the two sides of the peninsula may exceed 8°C. One would, therefore, expect the Cape Peninsula to provide a significant biogeographical barrier. However, Brown and Jarman noted that 57% of the invertebrate species present in False Bay are also present along the Atlantic coast of the peninsula. This is also true for opisthobranch gastropods, where at least 69.4% of the species present in False Bay are also present along the Atlantic coast. Brown and Jarman suggested that the area from False Bay to Cape Agulhas can be considered as transitional between cold and warm temperate faunas. Of the species of opisthobranchs present at Knysna, to the east of Cape Agulhas, 59% are also found along the Atlantic coast of the Cape Peninsula. There appears to be little change in the opisthobranch fauna between the Atlantic coast of the Cape

Peninsula and the warm temperate region. Rather, there appears to be a gradual dropping out and replacement of species. Millard (1978) found even less difference between the cold and warm-water temperate hydroid faunas in southern Africa than found here for opisthobranchs.

The same can be stated with regard to the boundary between the subtropical and tropical east coast provinces. There appears to be considerable similarity between the faunas present at Umgazana, Durban and Sodwana Bay. Approximately 80% of the species found at Umgazana and Durban are also found at Sodwana Bay. Clearly, Durban and Umgazana represent attenuations of the tropical fauna and have few opisthobranchs which are unique to them.

The differences in provincial overlap for opisthobranchs can best be summarized by comparison of Jaccard's Coefficient of Similarity (Valentine, 1966) between areas (Table 1). The greatest faunistic difference between adjacent areas occurs between Port Elizabeth and Umgazana. This difference corresponds to the shift between largely endemic and Atlantic species in temperate waters to Indo-Pacific and circumtropical species in the subtropics and tropics (Fig. 2).

Valentine (1966) calculated Jaccard's coefficients for adjacent faunistic provinces and subprovinces along the Pacific coast of North America. When values for southern African opisthobranchs are compared with these it is apparent that most adjacent areas appear to approach the subprovincial levels described by Valentine. The notable exception to this is the temperate/tropical boundary present between Port Elizabeth and Umgazana.

Stephenson *et al.* (1937) described the Cape Peninsula as one of the few places in the world "where water of such different temperature is separated by so little land." It

Table 1. Coefficients of faunistic similarity between areas.

	FB	KN	PE	UM	DU	SO
CT	.60	.45	.34	.09	.05	.02
FB	—	.59	.48	.14	.09	.05
KN	—	—	.54	.21	.10	.08
PE	—	—	—	.33	.19	.12
UM	—	—	—	—	.47	.26
DU	—	—	—	—	—	.63

is, therefore, remarkable that the greatest faunistic differences do not correspond to this area of profound physical oceanographic divergence, but rather to the break between temperate and tropical species between Port Elizabeth and Umgazana. The provincial boundaries in southern Africa appear to vary between higher taxa. For this reason, it is not particularly informative to stress provincial boundaries, but rather to regard them as convenient generalizations that can be employed to subdivide the biota.

RELATIONSHIPS OF INDO-PACIFIC TAXA WITHIN TROPICAL SOUTHERN AFRICA

Recent studies of the biogeography of marine organisms in the Indian and Pacific Oceans have focused on the consideration of possible vicariant events that isolated organisms inhabiting the Pacific Plate from those inhabiting the Indo-West Pacific (Kay, 1980, 1984; Springer, 1982; Kohn, 1983). Springer, in particular, has suggested that tectonic activity between the Pacific and Indian-Australian Plates has isolated the regions from each other, resulting in subsequent speciation. Newman (1987) suggested that changes in sea level, rather than tectonic events, could have been the primary isolating mechanisms of faunas on the Pacific Plate. Springer (1982) suggested that about 20-25% of the shorefish species present on the Pacific Plate are endemic to the plate. Kay (1979) noted that approximately 20% of the Hawaiian molluscan fauna is endemic to the islands. She (1984) provided an average estimate of endemism of marine organisms on the Pacific Plate at about 40% of the total fauna, based on data for a small sample of taxa which have been well studied. Included in this figure is 52% of the fish fauna, a significantly higher level of plate endemism than suggested by Springer. Data available for Pacific Plate opisthobranchs (Er. Marcus and Burch, 1965; Kay, 1967, 1979; Kay and Young, 1969; Gosliner, 1980; Bertsch and Johnson, 1981; Johnson and Boucher, 1984) suggest that approximately 20% of the species are endemic to the plate. The extent of Pacific Plate endemism is poorly understood for most groups of marine organisms. In many cases it is not known whether endemic species are widespread on the plate or whether they are limited to a single archipelago or island. More data are required to shed light on this significant issue.

The Indo-Pacific faunal component of the southern African opisthobranch fauna exhibits a distinct distributional pattern. Eighteen percent of the species are known only from the western Indian Ocean. The other 82% of the species present in southern Africa are also known to occur at the eastern extreme of the Indian Ocean. Fifty-seven percent of the southern African Indo-Pacific opisthobranchs also are found on the non-marginal portions of the Pacific Plate. This figure attests to the fact that many of the species known to occur in southern Africa are exceedingly widespread tropical taxa.

Although 18% of the opisthobranchs species appear to be restricted to the western Indian Ocean, insufficient data are presently available to authoritatively calculate the extent of the range of some species. For example, *Chromodoris anulata* Eliot was believed to be restricted to the western Indian Ocean, from the Red Sea to South Africa (Rudman, 1973a).

Recently, however, it has been recorded from the Gulf of California (Bertsch and Kerstitch, 1984).

Despite possible inaccuracies, the similarity in the extent of the range of southern African opisthobranch and prosobranch species within the Indo-Pacific, is noteworthy. Based on records of Indo-Pacific prosobranchs previously recorded from southern Africa, 23% appear to be restricted to the western Indian Ocean, 76% are found eastward to the western margin of the Pacific Plate and 59% of the total extend into the non-marginal portions of the Pacific Plate.

SISTER GROUP RELATIONSHIPS AND VICARIANCE IN SOUTHERN AFRICAN OPISTHOBRANCHS

The fact that the marine biota of southern Africa shares species with the North Atlantic, the sub-Antarctic and the Indo-Pacific is well established (Brown and Jarman, 1978; Kensley, 1981; Kilburn and Rippey, 1982). Kilburn and Rippey (1982) suggested that only 1-2% of the mollusk species within the region are also known from other southern oceanic regions. This figure is based solely on present distributional patterns of extant species and does not reflect historical events. When one examines the present distributions of the opisthobranch species of southern Africa, we find that none of the species present in the region are also found in other southern ocean localities. However, when we examine the probable sister species of the endemic opisthobranch species, a different pattern emerges. Probable sister species can be inferred with some degree of confidence for 48 of the 77 endemic species of opisthobranchs (Table 2). In several cases the inferences are easy to make (e.g. species of *Gargamella* are found only in the Sub-Antarctic and southern Africa). In other cases sister species have been determined on the basis of synapomorphies determined by methods described by Gosliner and Ghiselin (1984). Of these sister species, 25% are Indo-Pacific, 31% are known from other southern oceanic regions and 43% are known from the North Atlantic. These data suggest that, while there is currently little interchange with other southern cold-temperate and sub-Antarctic oceans, in the past southern Africa shared a significant number of species with the sub-Antarctic. Similarly, phylogenetic and biogeographical links with the Indo-Pacific have probably been present for a considerable period and have persisted to the present.

When considering vicariant events and their roles in producing various distributional patterns, most recent biogeographers have been primarily concerned with plate tectonic events as isolating mechanisms. The sister group relationships of the endemic species to sub-Antarctic species, with no extant species exhibiting this distributional pattern, suggests that this vicariant event could have occurred prior to those that isolated southern African species from conspecifics in the Indo-Pacific or North Atlantic. While these speciation events could be correlated with the breaking up of Gondwanaland, another hypothesis could better explain the Sub-Antarctic sister group relationships of these species. Newman (1979) has hypothesized that barnacle distributions in the southern oceans became established long after the

Table 2. Possible sister species of southern African endemics.

South African endemic	Sister species	Sister species range
<i>Ringicula turtoni</i> Bartsch	<i>R. australis</i> Hinds	Indo-Pacific
<i>Melanochlamys</i> sp.	<i>M. seurati</i> (Vayssière)	Mediterranean
<i>Philinopsis capensis</i> (Bergh)	<i>P. cyanea</i> (Martens)	Indo-Pacific
<i>Gastropeteron flavobrunneum</i> Gosliner	<i>G. pohnpei</i> Hoff and Carlson	Indo-Pacific
<i>G. alboaurantium</i> Gosliner	<i>G. pohnpei</i> Hoff and Carlson	Indo-Pacific
<i>Haminoea alfredensis</i> Bartsch	<i>H. navicula</i> (de Costa)	N. Atlantic
<i>Oxynoe</i> sp.	<i>O. viridis</i> (Pease)	Indo-Pacific
<i>Apysiosipsa sinusmensalis</i> (Macnae)	<i>A. formosa</i> Pruvot-Fol	Mediterranean
<i>Bursatella leachii africana</i> (Engel)	<i>B. leachii leachii</i> (Blainville)	Indo-Pacific
<i>Berthella</i> sp.	<i>B. sideralis</i> (Lovén)	N. Atlantic
<i>Pleurobranchus nigropunctatus</i> (Bergh)	<i>P. albiguttatus</i> (Bergh)	Indo-Pacific
<i>Pleurobranchaea bubala</i> Ev. Marcus and Gosliner	<i>P. tarda</i> Verrill	N. Atlantic
<i>Geitodoris capensis</i> Bergh	<i>G. planata</i> (Alder and Hancock)	N. Atlantic
<i>Aphelodoris brunnea</i> Bergh	<i>A. varia</i> (Abraham)	N.S.W. Australia
<i>A.</i> sp.	<i>A. luctuosa</i> Bergh	New Zealand
<i>Gargamella</i> sp. 1	<i>G. latior</i> Odhner	S. America
<i>G.</i> sp. 2	<i>G. latior</i> Odhner	S. America
<i>Rostanga</i> sp.	<i>Boreodoris setidens</i> Odhner	N. Atlantic
<i>Aldisa benguelae</i> Gosliner, in Millen and Gosliner	<i>A. banyulensis</i> Pruvot-Fol	N. Atlantic
<i>Aldisa trimaculata</i> Gosliner, in Millen and Gosliner	<i>A. zetlandica</i> (Alder and Hancock)	N. Atlantic
<i>Ceratosoma</i> sp.	<i>C. brevicaudatum</i> Abraham	s. Australia
<i>Chromodoris</i> sp.	<i>C. splendida</i> (Angas)	s. Australia
<i>Hypselodoris capensis</i> (Barnard)	<i>H. carnea</i> (Bergh)	Indo-Pacific
<i>Dendrodoris caesia</i> (Bergh)	<i>D. grandiflora</i> (von Rapp)	N. Atlantic
<i>Corambe</i> sp.	<i>C. testudinaria</i> Fischer	N. Atlantic
<i>Goniodoris mercurialis</i> Macnae	<i>G. castanea</i> Alder and Hancock	N. Atlantic
<i>Trapania</i> sp.	<i>T. lineata</i> Haefelfinger	N. Atlantic
<i>Polycera capensis</i> Quoy and Gaimard	<i>P. quadrilineata</i> Müller	N. Atlantic
<i>Lecithophorus capensis</i> Macnae	<i>Paliolla cooki</i> (Angas)	s. Australia
<i>L.</i> sp.	<i>P. cooki</i> (Angas)	s. Australia
<i>Tambja capensis</i> (Bergh)	<i>T. morosa</i> (Bergh)	Indo-Pacific
<i>Acanthodoris</i> sp.	<i>A. mollicella</i> Abraham	Auckland Is.
<i>Melibe rosea</i> Rang	<i>M. australis</i> (Angas)	s. Australia
<i>Melibe liltvedii</i> Gosliner	<i>M. australis</i> (Angas)	s. Australia
<i>Leminda millecra</i> Griffiths	<i>Telarma antarctica</i> Odhner	Antarctica
<i>Dermatobranchus</i> sp. 1	genus restricted to Indo-Pacific	
<i>D.</i> sp. 2	genus restricted to Indo-Pacific	
<i>Bonisa nakaza</i> Gosliner	<i>Galeoanulus ionnae</i> Miller	New Zealand
<i>Janolus capensis</i> Bergh	<i>J. novozealandica</i> (Eliot)	New Zealand
<i>J. longidentatus</i> Gosliner	<i>J. novozealandica</i> (Eliot)	New Zealand
<i>Flabellina capensis</i> (Thiele)	<i>F. lineata</i> (Alder and Hancock)	N. Atlantic
<i>F. funeka</i> Gosliner and Griffiths	<i>F. affinis</i> (Gmelin)	Mediterranean
<i>F.</i> sp.	<i>F. albomarginata</i> (Miller)	New Zealand
<i>Cuthona speciosa</i> (Macnae)	<i>C. caerulea</i> (Montagu)	N. Atlantic
<i>Facelina olivacea</i> Macnae	<i>F. bostoniensis</i> (Couthouy)	N. Atlantic
<i>Caloria</i> sp.	<i>C. elegans</i> (Alder and Hancock)	N. Atlantic
<i>Amanda armata</i> Macnae	<i>Nanuca sebastiani</i> Er. Marcus	N. Atlantic
<i>Cratena capensis</i> Barnard	<i>C. peregrina</i> (Gmelin)	Mediterranean

fragmentation of Gondwanaland and are largely a result of dispersal, followed by subsequent vicariance. The same could also be true of most other marine taxa in the southern hemisphere.

Tankard and Rogers (1978), Hendey (1981) and Olson (1983) have described the paleoecology of the Atlantic coast of South Africa during the Miocene and early Pliocene. Their studies of vertebrate fossils indicate that in the Miocene subtropical environments were present along the coast. During

the early Pliocene, ocean temperatures began to drop markedly and the terrestrial environment became significantly drier. Fossil sea birds from the Pliocene (Olson, 1983) include many taxa that are today present in the sub-Antarctic but are absent from southern Africa. It is likely that during this period many species of marine organisms were widely distributed throughout the southern oceans. Vicariant events, such as oceanic warming during portions of the Pleistocene, could have served as isolating mechanisms that resulted in

speciation within these widely distributed sub-Antarctic species.

When one examines the species that presently have disjunct distributions between southern Africa and the northern Atlantic, such as *Limacia clavigera* (Müller) and *Tritonia nilsodhneri* Ev. Marcus, and the species that have sister group relationships to the North Atlantic [e.g. *Flabellina capensis* with *F. lineata* and *F. browni* (Picton)], one finds that tectonic explanations cannot account for this vicariance. Populations of species present in southern Africa are geographically isolated and disjunct from those in the North Atlantic and are here considered to be relictual. A similar situation exists on both sides of the Isthmus of Panama, where many opisthobranch species have populations that are clearly isolated yet recognizable speciation has not occurred. The cold water environment along the Atlantic coast of southern Africa appears to be a relatively recent phenomenon. Late Pleistocene molluscan assemblages along the Atlantic coast of southern Africa suggest strong biogeographical links with West Africa and the Mediterranean (Tankard, 1975). The fact that many extant species of southern African opisthobranchs are also present in the North Atlantic indicates that little speciation has taken place and suggests that the isolation of the populations represents a relatively recent event. Several of the Atlantic species, such as *Retusa truncatula* and *Polycera quadrilineata*, are absent from the Atlantic coast of southern Africa and are restricted to warmer temperate waters of the region. This is further suggestive that these species are warm water relicts within southern Africa and implies that major climatic shifts by means of changes in oceanic currents could have a profound effect upon the evolution of marine faunas.

COMPARISON OF LEVELS OF ENDEMISM OF OPISTHOBRANCHS WITH OTHER SOUTHERN AFRICAN MARINE TAXA

Brown and Jarman (1978) demonstrated that within the southern African marine biota there are notable differences in biogeographical relationships between different taxa. For example, polychaete annelids within False Bay exhibit low levels of endemism (37.3% of the species are endemic) while echinoderms exhibit a high degree of endemism (82.4%). Similarly, Kensley (1983) has shown marked differences between the amphipod, isopod and decapod crustacean faunas. When one compares the data available for other mollusks (Kilburn and Rippey, 1982) with those for opisthobranchs, one finds that there are some significant differences (Figs. 2, 3). The non-opisthobranch mollusks exhibit a high level of endemism throughout all of southern Africa, while in the opisthobranchs there is a marked shift from endemic to Indo-Pacific species between the warm temperate and tropical regions. Even where endemism is high among opisthobranchs, it is significantly less than in non-opisthobranchs. Similarly, the percentage of Atlantic and Indo-Pacific species of non-opisthobranchs is much lower in every region than in opisthobranchs. In general, opisthobranchs within southern Africa appear to be more widespread than are other mollusks. This difference does not appear to be a taxonomic artifact,

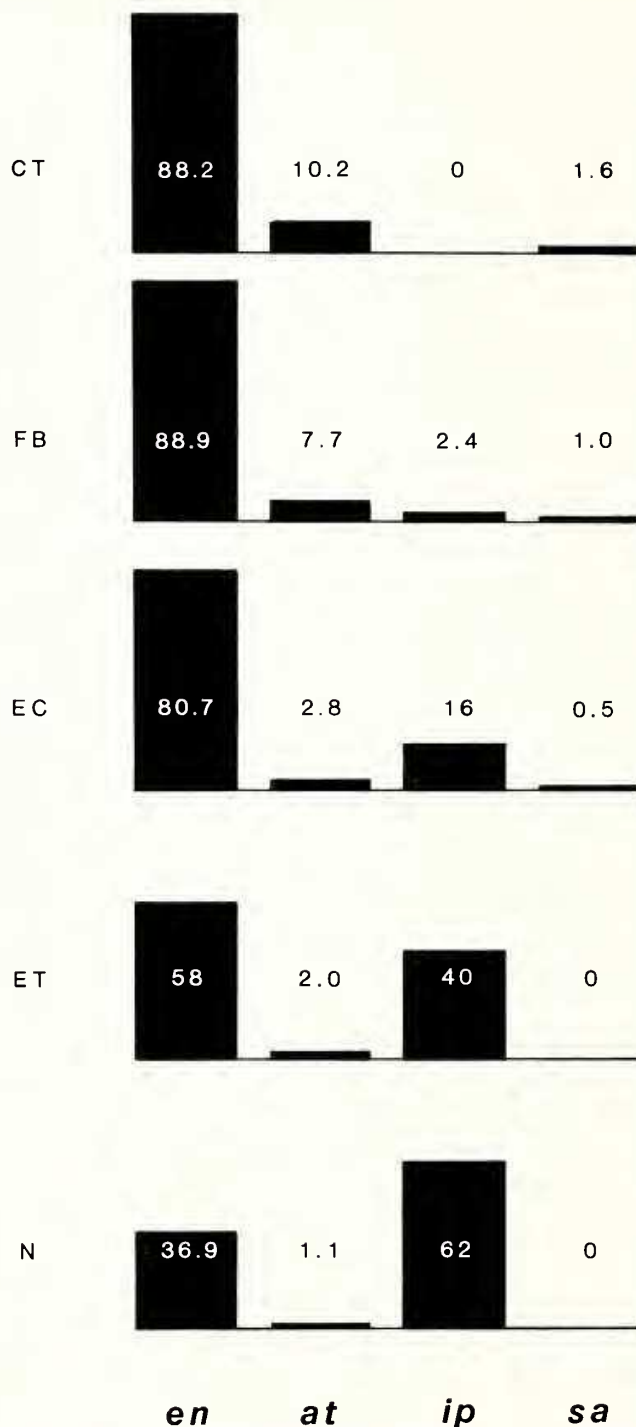


Fig. 3. Biogeographical affinities of southern African prosobranchs and bivalves (data extracted from Kilburn and Rippey, 1982) (CT - Cape Town, FB - False Bay, EC - East Cape, ET - Eastern Transkei, N - Natal, en - endemic, at - Atlantic, ip - Indo-Pacific, sa - South American/South Atlantic islands).

as the systematics of prosobranchs and opisthobranchs within the region are at about the same level of refinement.

Comparable differences in levels of endemism be-

tween molluscan taxa have been previously noted in southern Africa. Kilburn and Rippey (1982) noted that the Cypraeidae of western Transkei are largely Indo-Pacific while the Conidae of the same region are largely endemic. Similar biogeographical differences between taxa have been described from other regions of the world. Kay (1984) described less endemism among Hawaiian bivalves than among gastropods. She presented many other documented cases of divergent biogeographical affinity in a variety of organisms from throughout the Indo-Pacific.

Distinct distributional patterns between different opisthobranch taxa have been previously described. Bertsch (1972) noted that within the Panamic Province a large proportion of anaspidean opisthobranchs have circumtropical ranges while other taxa such as nudibranchs and cephalaspideans are distributed over a much narrower geographical range. Anaspideans, which are relatively well studied, appear to be more widespread in their distributions than other opisthobranch taxa.

These facts are suggestive of variable degrees of isolation of different taxa and imply that within the marine realm it is difficult to apply a single series of vicariant events to explain the biogeographical history of the entire biota.

LEVELS OF ENDEMISM AND THE TESTING OF VICARIANT HYPOTHESES

Nelson and Platnick (1981) have discounted the significance of disparity in levels of endemism (proportion of species of a particular taxon that are endemic to a region) between higher taxa and their role in explaining differences in vicariant history. They suggested that most differences in levels of endemism are merely taxonomic artifacts of lumping versus splitting. They further suggested (p. 489), that with greater taxonomic precision, "one might expect that most native Hawaiian marine organisms might ultimately be regarded as endemic, as is the case for land plants." Kay (1980) stated that there are qualitative differences between the levels of endemism of marine and terrestrial biota of the Hawaiian Islands and more recently (1984) contradicted Nelson and Platnick's assertion, noting that Hawaiian marine endemics have undergone little or no adaptive radiation.

Scheltema (1971a), Scheltema and Williams (1983) and Kay (1980, 1984) have noted differences in dispersal capabilities of marine organisms and have correlated these with biogeographical distributions. As one could predict, species with direct development are far less widely distributed than species with planktotrophic larvae. Kempf (1981) demonstrated that at least one species of opisthobranch can maintain viable larvae in the plankton in excess of 200 days. Springer (1982) suggested that in Indo-Pacific reef fishes, species with non-planktonic development can be as widely distributed as those with planktonic larvae. The correlation between life history adaptations and distribution requires more study.

Data available for southern African marine mollusks shed some light on the issue. There are differences in the levels of endemism between prosobranch and opisthobranch gastropods (Figs. 2, 3) within the region and these differences

occur at all seven localities surveyed within southern Africa. If one examines the life history modes of prosobranchs and opisthobranchs there are also notable differences. Southern African prosobranch gastropods exhibit a higher incidence of direct development and species with a short larval life than do opisthobranchs. Most prosobranch taxa possess representatives with direct, lecithotrophic and planktotrophic development (e.g. Littorinidae, Neritidae, Fissurellidae, Vermetidae, Crepidulidae). In other families, such as the Buccinidae, Marginellidae and Volutidae, direct development is the dominant mode of development. Even in prosobranch taxa where planktotrophic development is generally the rule, many southern African representatives possess direct development. This is the case in the Cypraeidae (Gosliner and Liltved, 1985) and the Conidae (Kilburn and Rippey, 1982). In contrast, of the two hundred opisthobranch species studied in southern Africa, only one is known to possess direct development (Gosliner and Griffiths, 1981). Thus, there is a strong correlation between length of larval life and levels of endemism in southern African marine mollusks.

Similarly, Kensley (1983) has shown that decapod crustaceans exhibit less endemism in southern Africa than do amphipods and isopods. Most decapods have pelagic larval stages while most amphipods and isopods brood their young. The polychaete annelids in southern Africa have a low degree of endemism. The overwhelming number of species have pelagic larvae and are widely distributed.

Nelson and Platnick (1981) stated that levels of endemism are irrelevant with regard to the cladistic aspect of biogeography. This does not appear to be the case in the southern African marine biota. As noted above, the endemic Cypraeidae of southern Africa, in species where it has been studied, all have direct development (Gosliner and Liltved, 1985). This appears to be a synapomorphy, which together with morphological data, unites the southern African taxa with their sister group in southern Australia. In this case, at least, life history strategies, sister group relationships and levels of endemism are all strongly linked. Levels of endemism are significant in biogeographical studies and differences in endemism could have strong biological and cladistic bases.

Life history modes may not be the only biological bases for producing differences in levels of endemism. Stanley (1979) suggested that there could be a correlation between patterns of extinction and degree of endemism. He has also examined variable rates of speciation between bivalves and gastropods. Kay (1984) has discussed some of these other possible reasons for discordance in biogeographical data.

Vicariance biogeographers (Nelson and Platnick, 1981) claim to construct and test hypotheses of biogeographical relationships. To discount major differences in levels of endemism between taxa as mere artifacts of taxonomy is subjective judgement without factual support. One cannot simply discard data that challenge an hypothesis. As Kay (1980) pointed out, the fact that 94% of the vascular flora and 80-90% of the terrestrial mollusks are endemic to Hawaii while only 20% of the marine mollusks are endemic, suggests that evolution of marine and terrestrial organisms has been influenced by different degrees of isolation. This fact also

suggests that different vicariant events could have been important in the marine environment than in terrestrial ecosystems. If vicariance biogeographers wish to have their hypotheses taken seriously, they will have to regard such discrepancies of data as serious challenges to simplistic hypotheses rather than artifacts of human perception of systematics.

Vicariance biogeographers suggest that the only considerations to be utilized in biogeographical analysis are the determination of sister species of endemic species and their distributional patterns. There are several flaws with employing this approach to the exclusion of other pertinent data. Species that have disjunct distributions but have not yet speciated also supply information that has a direct bearing on vicariant events and biogeographical history. Consideration of only endemic species becomes potentially problematic in regions with low levels of endemism, where the likelihood that a small number of endemics and their sister species may not adequately reflect the recent vicariant events that have occurred. It appears that a more eclectic approach, integrating vicariance biogeography and present distributional patterns, with a serious attempt to incorporate biological factors that could alter those patterns, will produce a far more coherent picture of the biogeography of organisms.

ACKNOWLEDGMENTS

The following individuals kindly read the manuscript and provided valuable suggestions for its improvements in both style and content: Hans Bertsch, William Fink, Michael Ghiselin, Brian Kensley, William Newman, Rudolf Scheltema, Victor Springer and Gary Williams. I also thank Barbara Weitbrecht for preparing the final figures. This research was supported by the South African Museum, the Council for Scientific and Industrial Research of South Africa, a Smithsonian Postdoctoral Fellowship and the In-house Research Fund of the California Academy of Sciences.

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- Appendix 1.** Distributions of southern African Opisthobranchs. Listed below are the taxa that have sufficiently reliable distributional data to infer biogeographical relationships. For each species its distribution outside of southern Africa is presented as A-Atlantic, CO-Cosmopolitan, CT-Circumtropical, E-Endemic or IP-Indo-Pacific. Its range is then presented. For species with Indo-Pacific distributions the known eastern limit of its distribution is presented in parentheses. Immediately following the distribution outside of southern Africa is an indication of the distribution of each species within southern Africa. The following numerals indicate geographical regions within southern Africa and correspond to those of Figure 1: 1-Cape Town; 2-False Bay; 3-Knysna; 4-Port Elizabeth; 5-UmgaZana; 6-Durban; 7-Sodwana Bay. A species with a range of 3-7 is known from the Knysna region to the Sodwana Bay area.
- Class Gastropoda
Subclass Opisthobranchia
- Order Cephalaspidea
Family Ringiculidae
Ringicula turtoni Bartsch, 1915, E, 4-7.
- Family Acteonidae
Acteon flammeus (Gmelin, 1791), IP (Fiji), 6-7.
A. fortis Thiele, 1925, IP (East Africa), 6-7.
Pupa affinis (A. Adams, 1854), IP (Arabian Sea), 6-7.
P. solidula (Linnaeus, 1758), IP (Tahiti), 6-7.
P. sulcata (Gmelin, 1791), IP (Fanning Island), 6-7.
P. suturalis (A. Adams, 1854), IP (Madagascar), 6-7.
P. tessellata (Reeve, 1842), IP (Hawaii), 6-7.
Rictaxis albus (Sowerby, 1873), E, 2-7.
- Family Bullinidae
Bullina lineata (Gray, 1825), IP (Hawaii), 5-7.
- Family Hydatinidae
Hydatina albocincta (van der Hoeven, 1811), IP (Hawaii), 6-7.
H. amplustre (Linnaeus, 1758), IP (Hawaii, Tahiti), 6-7.
H. physis (Linnaeus, 1758), CT (Caribbean, IP to Hawaii), 6-7.
H. zonata (Lightfoot, 1786), IP (Japan), 6-7.
Micromelo undata (Brug  re, 1792), CT (Caribbean, IP to Hawaii), 6-7.
- Family Retusidae
Retusa truncatula (Brug  re, 1792), A (European Atlantic, Canary Is), 2-6.
- Family Scaphandridae
Acteocina smithi (Bartsch, 1915), E, 4-7.
Cylichna tubulosa Gould, 1859, E, 1-6.
Scaphander punctostriatus (Mighels, 1841), A (W. and E. Atlantic), 1.
- Family Aglajidae
Chelidonura fulvipunctata Baba, 1938, CT (Mediterranean, IP to Japan), 3-7.
C. hirundinina (Quoy and Gaimard, 1824), CT (Caribbean, IP to Hawaii), 5-7.
Melanochlamys sp., E, 2.
Philinopsis capensis (Bergh, 1907), E, 2-4.
P. cyanea (Martens, 1879), IP (Australia), 6-7.
- Family Gastropteridae
Gastropteron alboaurantium Gosliner, 1984, E, 1.
G. flavobrunneum Gosliner, 1984, E, 1.
- Family Haminoeidae
Atys cylindrica (Helbling, 1779), IP (Fanning Island), 6-7.
Haminoea alfredensis Bartsch, 1915, E, 1-4.
H. natalensis (Krauss, 1848), IP (Seychelles), 5-7.

- Phanerophthalmus smaragdinus* (Rüppell and Leuckart, 1831), IP (Easter Is.), 7.
Smaragdina calyculata (Broderip and Sowerby, 1829), IP (Easter Is.), 7.
- Family Bullidae
Bulla ampulla (Linnaeus, 1758), IP (Central Pacific), 4-7.
- Order Sacoglossa
 Family Cylindrobullidae
Ascobulla fischeri (Adams and Angas, 1864), IP (Australia), 2-7.
Volvatella laguncula Sowerby, 1894, E, 2-4.
- Family Juliidae
Berthellina schlumbergeri Dautzenberg, 1895, IP (Hawaii), 7.
Julia zebra Kawaguti, 1981, IP (Easter Is.), 7.
- Family Oxynoidae
Lobiger souverbiei Fischer, 1856, CT (Caribbean, Mediterranean, IP to Pacific North America), 7.
Lophopleurella capensis (Thiele, 1912), E, 2.
Oxynoe viridis (Pease, 1861), IP (Pacific North America), 6-7.
O. sp., E, 2-3.
- Family Elysiidae
Elysia halimeda Macnae, 1954, IP (Hawaii), 5-7.
E. livida Baba, 1955, IP (Enewetak), 7.
E. marginata (Pease, 1871), IP (Fanning Is.), 6-7.
E. moebii (Bergh, 1888), IP (Mauritius), 7.
E. rufescens (Pease, 1871), IP (Tahiti), 7.
E. vatae Risbec, 1928, IP (Enewetak), 7.
E. virgata (Bergh, 1888), IP (Mauritius), 7.
E. viridis (Montagu, 1804), A (European Atlantic, Mediterranean), 1-6.
- Family Stiligeridae
Placida dendritica (Alder and Hancock, 1843), CO (W. and European Atlantic, Mediterranean, Japan, Australia, California), 1-4.
Stiliger ornatus Ehrenberg, 1831, IP (Japan), 7.
- Family Caliphyllidae
Aplysiopsis sinusmensalis (Macnae, 1954), E, 1-2.
Phyllobranchillus orientalis (Kelaart, 1858), IP (Hawaii), 6-7.
- Order Anaspidea
 Family Akeridae
Akera soluta (Gmelin, 1791), IP (Enewetak), 3-7.
- Family Aplysiidae
Aplysia dactylomela Rang, 1828, CT (Caribbean, Ghana, IP to Pacific North America), 4-7.
A. juliana Quoy and Gaimard, 1832, CT (Caribbean, Ghana, IP to Pacific North America), 1-7.
A. oculifera Adams and Reeve, 1850, IP (Hawaii), 2-7.
A. parvula Mörch, 1863, CT (W. and E. Atlantic, IP to Pacific North America), 1-7.
Dolabella auricularia (Solander, 1786), IP (Pacific North America), 3-7.
- Family Notarchidae
Bursatella leachii leachii (Blainville, 1817), IP (New Zealand), 6-7.
B. leachii africana (Engel, 1927), E, 2-4.
Dolabrifera dolabrifera (Rang, 1828), CT (Caribbean, Ghana, IP to Pacific North America), 6-7.
Stylocheilus longicauda (Quoy and Gaimard, 1824), CT (Caribbean, IP to Pacific North America), 5-7.
- Order Notaspidea
 Family Umbraculidae
Tylodina alfredensis Turton, 1932, E, 4.
Umbraculum sinicum (Gmelin, 1783), CT (Caribbean, Mediterranean, IP to Pacific North America), 5-7.
- Family Pleurobranchidae
Berthella plumula (Montagu, 1803), A (European Atlantic, Mediterranean), 1-3.
B. tupala Marcus, 1957, CT (Caribbean, IP to Hawaii) 5.
B. sp., E, 1.
Berthellina citrina (Rüppell and Leuckart, 1828), IP (Hawaii), 1-7.
Pleurobranchus inhacae Macnae, 1962, IP (Mauritius), 6-7.
P. peronii Cuvier, 1805, IP (Hawaii), 6-7.
P. xhosa Macnae, 1962, IP (Seychelles), 5-7.
P. nigropunctatus (Bergh, 1907), E, 2-4.
- Family Pleurobranchaeidae
Euseloneops luniceps (Cuvier, 1817), IP (Hawaii), 7.
P. brockii Bergh, 1897, IP (East Africa), 7.
P. bubala Ev. Marcus and Gosliner, 1984, E, 1-3.
P. tarda Verrill, 1880, A (Atlantic North America, W. Africa), 1-3.
Pleurobranchella nicobarica Thiele, 1925, IP (Nicobares Is.), 7.
- Order Nudibranchia
 Suborder Doridacea
 Family Bathydorididae
Doriodoxa benthalis Barnard, 1963, E, 1.
- Family Dorididae
Atagema gibba Pruvot-Fol, 1951, A (European Atlantic, Mediterranean), 3.
A. rugosa Pruvot-Fol, 1951, A (Mediterranean), 1.
Doriopsis pecten (Collingwood, 1881), IP (Hawaii), 6-7.
Doris verrucosa Linnaeus, 1758, A (W. and E. Atlantic), 1-3.
D. sp., IP (Tanzania), 7.
- Family Discodorididae
Discodoris fragilis (Alder and Hancock, 1864), CT (Canary Is., IP to Hawaii), 5-7.
D. sp., E, 1-2.
Geitodoris capensis Bergh, 1907, E, 1-4.
- Family Asteronotidae
Aphelodoris brunnea Bergh, 1907, E, 2-4.
A. sp., E, 1-3.
Artachaea sp., E, 3.
Halgerda formosa Bergh, 1880, IP (Mauritius), 6-7.
H. punctata Farran, 1905, IP (Sri Lanka), 7.
H. wasinensis Eliot, 1904, IP (Enewetak), 7.
Sclerodoris apiculata (Alder and Hancock, 1864), IP (India), 5-7.
S. coriacea Eliot, 1904, (Tanzania), 7.
- Family Kentrodorididae
Gargamella sp. 1, E, 2.
G. sp., E, 2.
Jorunna tomentosa (Cuvier, 1804), A (European Atlantic), 1-3.
J. zania Marcus 1976, IP (Tanzania), 6-7.
- Family Rostangidae
Rostanga muscula (Abraham, 1877), IP (New Zealand), 6-7.
R. sp. 1, E, 1-2.
R. sp. 2, E, 1.
- Family Aldisidae
Aldisa benguelae Gosliner, in Millen and Gosliner, 1985, E, 1.
A. trimaculata Gosliner, in Millen and Gosliner, 1985, E, 1-2.
- Family Platydorididae

- Platydoriscus cruentus* (Quoy and Gaimard, 1832), IP (Enewetak), 6-7.
- P. scabra* (Cuvier, 1806), IP (Marshall Is.), 7.
- Family Chromodorididae
- Cadlina* sp. 1, E, 2.
- C.* sp. 2, E, 1.
- Ceratosoma cornigerum* A. Adams and Reeve, 1850, IP (Hawaii), 7.
- C.* sp., E, 3.
- Chromodoris africana* Eliot, 1904, (Red Sea, Seychelles), 7.
- C. alderi* Collingwood, 1881, IP (Formosa), 6-7.
- C. annulata* Eliot, 1904, IP (Gulf of California), 6-7.
- C. aspersa* (Gould, 1852), IP (Hawaii), 6-7.
- C. geometrica* (Risbec, 1928), IP (Enewetak), 7.
- C. hamiltoni* Rudman, 1977, IP (Tanzania), 6-7.
- C. inopinata* Bergh, 1905, IP (Fiji), 7.
- C. marginata* (Pease, 1860), IP (Hawaii), 6-7.
- C. vicina* Eliot, 1904, IP (Tanzania), 7.
- C.* sp. 1, E, 1-4.
- C.* sp. 2, E, 1.
- C.* sp. 3, IP (Tanzania), 7.
- C.* sp. 4, IP (Seychelles), 7.
- C.* sp. 5, IP (Seychelles), 7.
- Durvilledoris lemniscata* (Quoy and Gaimard, 1832), IP (Tahiti), 6-7.
- Glossodoris atromarginata* (Cuvier, 1804), IP (Tahiti), 7.
- G.* sp., IP (Tanzania), 7.
- Hypselodoris carnea* (Bergh, 1889), IP (Mauritius), 5-7.
- H. capensis* (Barnard, 1927), E, 1-5.
- H. infucata* (Rüppell and Leuckart, 1828), IP (Hawaii), 6-7.
- H. maridadii* Rudman, 1977, IP (Hawaii), 6-7.
- Noumea decussata* Risbec, 1928 (Hawaii), 5-7.
- N. purpurea* Baba, 1949, IP (Japan), 7.
- N. varians* (Pease, 1871), IP (Hawaii), 7.
- Risbecia pulchella* (Rüppell and Leuckart, 1828), IP (Red Sea), 6-7.
- Family Hexabranchidae
- Hexabranchus sanguineus* (Rüppell and Leuckart, 1828), IP (Hawaii), 5-7.
- Family Dendrodorididae
- Dendrodoris caesia* (Bergh, 1907), E, 1-4.
- D. denisoni* (Angas, 1864), IP (Hawaii), 6-7.
- D. nigra* (Stimpson, 1855), IP (Hawaii), 5-7.
- Doriopsilla miniata* (Alder and Hancock, 1864), CT (Mediterranean, IP to Australia), 1-7.
- D.* sp. 1, E, 1.
- D.* sp. 2, E, 1-3.
- Family Phyllidiidae
- Ceratophyllidia africana* Eliot, 1903, IP (Tanzania), 7.
- Phyllidia varicosa* Lamarck, 1801, IP (Hawaii), 6-7.
- P.* sp. 1, IP (Seychelles), 7.
- P.* sp. 2, IP (Seychelles), 7.
- Family Vayssieridae
- Okadaia elegans* Baba, 1930, IP (Hawaii), 5-7.
- Family Corambidae
- Corambe* sp., E, 2.
- Family Goniadoridae
- Ancula* sp., E, 1-2.
- Goniadoris castanea* Alder and Hancock, 1854, CO (European Atlantic, Mediterranean, Japan), 1-4.
- G. mercurialis* Macnae, 1958, E, 1-2.
- G. ovata* Barnard, 1934, E, 2.
- Okenia mediterranea* (Lhering, 1886), A (Mediterranean), 1-2.
- Trapania* sp., E, 3.
- Family Polyceridae
- Aegires* sp., E, 1-4.
- Crimora* sp., E, 4.
- Kalinga ornata* Alder and Hancock, 1864, IP (Australia), 6-7.
- Kaloplocamus ramosus* (Cantraine, 1835), CT (Mediterranean, IP to Australia), 2-7.
- Limacia clavigera* (Müller, 1776), A (European Atlantic, Mediterranean), 1-4.
- Plocamopherus maculatus* (Pease, 1860), IP (Hawaii), 7.
- Polycera capensis* Quoy and Gaimard, 1824, E (introduced in Australia), 1-4.
- P. hedgpethi* Er. Marcus, 1964, IP (Australia, New Zealand, Pacific North America), 3.
- P. quadrilineata* (Müller, 1776), A (E. Atlantic, Mediterranean), 3-4.
- Thecacera pacifica* (Bergh, 1884), IP (Arafura Sea), 3-7.
- T. pennigera* (Montagu, 1804), CO (W. and E. Atlantic, Mediterranean, Ghana, Pakistan, Australia, New Zealand, Japan), 1-5.
- Nembrotha lineolata* Bergh, 1905, (Japan), 6-7.
- N. livingstonei* Allan, 1933, IP (Australia), 6-7.
- Roboastra gracilis* (Bergh, 1877), IP (Australia), 7.
- R. luteolineata* (Baba, 1936), IP (Japan), 7.
- Tambja capensis* (Bergh, 1907), E, 1-4.
- T. morosa* (Bergh, 1877), IP (Hawaii), 7.
- Family Gymnodorididae
- Gymnodoris alba* (Bergh, 1877), IP (Hawaii), 6-7.
- G. bicolor* (Alder and Hancock, 1864), IP (Hawaii), 7.
- G. ceylonica* (Kelaart, 1858), IP (Tahiti), 7.
- G. inornata* (Bergh, 1880), IP (Japan), 6-7.
- G. okinawae* Baba, 1936, IP (Hawaii), 7.
- Lecithophorus capensis* Macnae, 1958, E, 1-4.
- Family Onchidorididae
- Acanthodoris* sp., E, 2.
- Family Bornellidae
- Bornella stellifer* (Adams and Reeve in A. Adams, 1848) IP (Hawaii), 5-7.
- B. anguilla* Johnson, 1983, IP (Enewetak), 7.
- Family Scyllaeidae
- Notobryon wardi* Odhner, 1936, IP (Australia), 1-3.
- Family Tethyidae
- Melibe pilosa* Pease, 1860, IP (Hawaii), 7.
- M. rosea* Rang, 1829, E, 1-3.
- M. liltvedi* Gosliner, 1987, E, 1.
- Family Dotoidae
- Doto coronata* (Gmelin, 1791), A (E. Atlantic, Mediterranean), 1-3.
- D. pinnatifida* (Montagu, 1804), A (E. Atlantic, Mediterranean), 1-2.
- D. rosea* Trinchese, 1881, A (Mediterranean), 2.
- Family Marianinidae
- Marianina rosea* Pruvot-Fol, 1930, IP (Enewetak), 7.
- Family Tritoniidae
- Marionopsis cyanobranchiata* (Rüppell and Leuckart, 1831), IP (Japan), 5-7.
- Tritonia nilsodhneri* Ev. Marcus, 1983, A (European Atlantic), 1.
- T.* sp. 1, E, 2-4.
- T.* sp. 2, E, 1-3.
- Family Lemnidae
- Leminda millecra* Griffiths, 1985, E, 1-6.
- Family Arminidae
- Armina gilchristi* (Bergh, 1907), E, 1-4.
- Dermatobranchus* sp. 1, E, 1-4.
- D.* sp. 2, E, 1.

Family Janolidae

- Bonisa nakaza* Gosliner, 1981, E, 1-4.
Janolus capensis Bergh, 1907, E, 1-4.
J. longidentatus Gosliner, 1981, E, 1-2.

Family Flabellinidae

- Flabellina capensis* (Thiele, 1925), E, 1-4.
F. funeka Gosliner and Griffiths, 1981, E, 2-4.
F. sp. 1, E, 2.
F. sp. 2, E, 2.
F. sp. 3, IP (Enewetak), 7.

Family Embletoniidae

- Embletonia gracilis* Risbec, 1928, IP (Hawaii), 2.

Family Eubbranchidae

- Eubbranchus sp. 1*, E, 1-2.
E. sp. 2, E, 2-3.
E. sp. 3, E, 3.

Family Tergipedidae

- Catriona casha* Gosliner and Griffiths, 1981, E, 1-3.
Cuthona annulata (Baba, 1949), IP (Japan), 7.
C. kanga (Edmunds, 1970), IP (Tanzania), 7.
C. ornata Baba, 1937, IP (Japan), 6-7.
C. speciosa (Macnae, 1954), E, 1-4.
C. sp. 1, E, 1-2.
C. sp. 2, E, 1-2.
Phostilla melanobranchia Bergh, 1874, IP (Hawaii), 7.
Tergipes tergipes Forskäl, 1779, A (W. and E. Atlantic, Mediterranean), 1-2.

Family Fionidae

- Fiona pinnata* (Eschscholtz, 1831), CO (all warm temperate and

tropical seas), 3.

Family Facelinidae

- Amanda armata* Macnae, 1954, E, 1-2.
Caloria indica (Bergh, 1896), IP (Hawaii), 7.
C. sp. 1, E, 1-2.
C. sp. 2, E, 1.
Facelina olivacea Macnae, 1954, E, 1-4.
Favorinus ghanensis Edmunds, 1968, A (Ghana), 3.
F. japonicus Baba, 1949, IP (Hawaii), 7.
Godiva quadricolor (Barnard, 1927), A (Ghana), 1-4.
Moridilla brockii Bergh, 1888, IP (Sundu Sea), 7.
Phyllodesmium hyalinum Ehrenberg, 1831, IP (Okinawa), 7.
P. poindimiei (Risbec, 1928), IP (New Caledonia), 6-7.
P. serratum (Baba, 1949), IP (Japan), 2-7.
Pruvotfolia pselliotes (Labbe, 1923), A (Mediterranean, Ghana), 1-4.

Family Cratenidae

- Cratena capensis* Barnard, 1927, E, 1-4.
C. simba Edmunds, 1970, 7.
C. sp., E, 3.

Family Glaucidae

- Glaucus atlanticus* Forster, 1777, CT (all tropical and warm temperate oceans), 1-7.

Family Aeolidiidae

- Aeolidiella alba* Risbec, 1928, CT (Caribbean, IP to Pacific North America), 6-7.
A. indica Bergh, 1888, CT (Caribbean, Mediterranean, IP to Pacific North America), 1-7.
Baeolidida palythoe Gosliner, 1985, IP (Seychelles), 5-7.